

CANADIAN TRANSLATION OF FISHERIES AND AQUATIC SCIENCES

No. 4859

A quantitative analysis on the larval mortality by cannibalism
in....A study of comparative biology on Japanese
pisces to population analysis - III

by

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Original Title: Shigen kaiseki no tame no gyorui no hikaku
seibutsugakuteki kenkyu III. Tomogui ni yoru shoki
genmo ni kan-suru suryo kaiseki

From: Tokai-ku Suisan Kenkyusho Kenkyu Hokoku 100: 79-89, 1979.

Translated by the Translation Bureau (RAY/PS)
Multilingual Services Division
Department of the Secretary of State of Canada

Department of Fisheries and Oceans
Bedford Institute of Oceanography
Dartmouth, NS

1982

24 pages typescript



MULTILINGUAL SERVICES DIVISION - DIVISION DES SERVICES MULTILINGUES

TRANSLATION BUREAU

BUREAU DES TRADUCTIONS

LIBRARY IDENTIFICATION - FICHE SIGNALÉTIQUE

Translated from - Traduction de Japanese Into - En English CTFAS 4859

Author - Auteur KAWAI Tomoyasu & ISIBASI Kimiko

Title in English or French - Titre anglais ou français

A Quantitative Analysis on the Larval Mortality by Cannibalism
in....A Study of Comparative Biology on Japanese Pisces to Population
Analysis - III

Title in foreign language (Transliterate foreign characters)
Titre en langue étrangère (Transcrire en caractères romains)

Shigen Kaiseki no tame no Gyorui no Hikaku Seibutsugakuteki Kenkyu
III. Tomogui ni yoru Shoki Genmo ni kan-suru Suryo Kaiseki

Reference in foreign language (Name of book or publication) in full, transliterate foreign characters.
Référence en langue étrangère (Nom du livre ou publication), au complet, transcrire en caractères romains.

Tokai Suikenpo

Reference in English or French - Référence en anglais ou français

Bull. Tokai Reg. Fish. Res. Lab.

Publisher - Éditeur	DATE OF PUBLICATION DATE DE PUBLICATION			Page Numbers in original Numéros des pages dans l'original
	Year Année	Volume	Issue No. Numéro	79-89
Piece of Publication Lieu de publication	1979	100		Number of typed pages Nombre de pages dactylographiées 24

Requesting Department
Ministère-Client DFO

Translation Bureau No. 1035816
Notre dossier n°

Branch or Division
Direction ou Division Sci.Info.&Pub.Br.

Translation (Initials) RAY / PS
Traducteur (Initiales)

Person requesting
Demandé par Allan T. Reid

Your Number
Votre dossier n°

JUL 21 1982

Date of Request
Date de la demande 17 VI 82

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BUREAU DES TRADUCTIONS

Client's No.—N ^o du client	Department — Ministère Fisheries & Oceans	Division/Branch — Division/Direction S.I.P.B.	City — Ville Ottawa
Bureau No.—N ^o du bureau 1035186	Language — Langue Japanese	Translator (Initials) — Traducteur (Initiales) RAY / PS	JUL 21 1982

A Study of Comparative Biology on Japanese
Pisces to Population Analysis—III.

A Quantitative Analysis on the Larval Mortality by Cannibalism

Tomoyasu KAWAI and Kimiko ISIBASI

Abstract: Since the fishes having a feeding habit to eat fish, the fish eaters, particularly spawn a large number of eggs off shore where the nutriment level is lower than the coast, we formed a hypothesis that the biggest reason of their larval mortality is their own cannibalism. Analysing the relation between the mouth size of fish (D) and the body length (L) at the post larval stage, the rate D/L of the fish eaters reaches a maximum at that stage precisely and this relation supports our hypothesis morphologically.

We show a mathematical model on the stock size under the condition that the reason of larval mortality is only cannibalism, as follows;

$$W_n = W_0 \left(\frac{1+r}{2} \right)^n$$

where, W is the weight of fish stock, r the feeding efficiency and n the number of times of cannibalism. If the food abundance of larva is proportional to the time (t), the model will be shown as

$$W_t = W_0' \left(1 + \frac{r}{A} t \right)^n$$

where, A is the time interval between the first cannibalism and the second, $n = 1 - \{\log 2 / \log(1+r)\}$ and $W_0' = W_0(1+r)/2$.

When we use the information on yellowtail (*Seriola quinqueradiata*) for the value of parameters of the above mentioned models, we can obtain the survival rate in post larval stage as almost 1/1000 in number of fish, which is not so different from the former estimated rate.

Received: December 6, 1979 Tokai Reg. Fish. Res. Lab. Pub.

A-698

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SEC 5-25 (Rev. 81/11)

Canada

Information obtained to date on the larval mortality mechanisms of piscivorous fish

In Parts I and II of this series Kawai^{1),2)} inferred statistically that the feeding habits of marine Teleostei are an extremely important factor affecting their morphology, ecology, and occasionally even their physiology. The fish eaters in particular exhibit unique features in contrast to fishes with different feeding habits (plankton feeders, mixed food eaters) and given the view that while fish-eating may accelerate growth, it retards the time of maturation, it should not be ignored from the standpoint of the evolutionary history of fishes either. This fact provides an excellent explanation for the phenomenon, appearing at first glance to be a singular law of nature, that although the fish eaters are ordinarily large fish, they produce great quantities of small eggs (statistically on the same size level as those of fish with other feeding habits though) and hence small larvae grow larger at a more vigorous pace. //80

So, there is not strictly speaking an overwhelming abundance of fish eaters in the ocean. Obviously the numbers of fish eaters must be smaller than the stocks of fish they feed on. This means that the large quantities of eggs and young produced die at a far higher rate than in

other fish species. Hitherto it has been supposed that the normal causes of their larval mortality were unfavourable physical environments or a lack of food. The authors, however, have doubts about the following points.

(1) Stock fluctuations are generally more stable in large fish eaters than in plankton feeders, and the view that fish-eating larvae are easily affected by a poor physical environment does not stand up well. If they were in fact more easily affected than others, the fluctuations in fish-eating stocks would likely be greater.

(2) The spawning grounds of fish eaters are more commonly offshore, where the smaller organisms they feed on are scarcer than nearer the coast. Why, then, in a highly rationally constructed biological world, would the fish eaters alone have come to do something as absurd as producing great masses of eggs in food-deficient locations?

The authors wondered, assuming this outwardly ridiculous behaviour to be rational in fact with respect to the development of fish eaters, how it would work. If the hatched larvae, finding almost no small plankton available to feed on, could thus only expect to die to a fish, there would be no rhyme or reason to the selection of such spawning grounds. Perhaps there would be no other way of growing up there, logically,

except cannibalism. And, if their principal food was the fish school to which they themselves belonged, many of the apparently illogical phenomena observed hitherto reappear in a reasonable light. In other words, their larval mortality is not due to external factors and stock stability is enhanced; the relatively smaller size and larger numbers of eggs can be seen as logical in the context of food supply, and the comparatively stable physical environment offshore ensures the hatching conditions for the small, defenceless eggs. So, the authors' hypothesis is as follows;

"The main cause of mortality during the larval stage of many fish eating species which spawn comparatively far from shore and produce large quantities of small eggs is cannibalism by schools of hatched larvae of the same species".

It should be noted here that the authors do not intend to say that all fish eaters bar none are subject to the aforementioned conditions. In the first place, the definition of what constitutes a fish eating species has not yet been established, and at this stage one can make a determination only on the basis of the type of food consumed. Nevertheless, it is believed that many obviously piscivorous fishes, such as the yellowtails, skipjacks and tunas, characterized by the production of large masses of small eggs comparatively far from shore come under the purvey of the stated hypothesis.

Discussion of the plausibility of the hypothesis

The mechanisms of larval mortality of fish in the natural world remain within the realm of conjecture at the present stage, but the hypothesis described above by the authors may be somewhat of a departure from hitherto commonly accepted views. It would, therefore, seem fitting to give some consideration first to its actual plausibility before proceeding to a population analysis.

In fish nutrition is supplied by absorption of the yolk immediately upon hatching and ingestion from outside begins only in the late larval stage. Larval mortality during the so-called critical period may be taken as occurring in the period between the start of feeding and the ability to move by swimming is acquired, or until the onset of the larval stage. In other words, the interval directly after independence from the protective functions provided by the parent up to acquisition of the ability to function independently vis-à-vis the external world is the major larval mortality period, and an attempt was made to investigate morphologically on the basis of the literature whether or not the development of rampant cannibalism was possible among larvae of fish eaters during this period.

Materials and methods

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There are few reports on statistical studies of larval morphology for most fish species. The authors proposed to investigate the body lengths (total lengths) and mouth diameters categorized by feeding habits as early as possible in the post larval stage on the basis of the findings of Shirota³⁾ and Uchida et al⁴⁾ to observe the characteristics of the fish eaters and to enquire into the potential for cannibalism (Tables 1 and 2). Following Shirota, we used as the mouth diameter the distance between the jaws at 90° aperture (upper jaw length x $\sqrt{2}$). In data from Uchida et al the upper jaw length is not normally shown, so it has been estimated as a ratio of body length from illustrations of the larvae. For classification by feeding habits, those of the adult fish were used, after Kawai²⁾.

Results and discussion

The authors first proceeded to examine any variations in mouth diameter in the post larval stage according to the feeding habits of the various species. On the basis of Tables 1 and 2 a larval body length of several millimetres and a mouth diameter in the vicinity of 10% of the length (several microns) were found to be the norm. When the figures from both Shirota and Uchida et al are broken down by the feeding habits of the fish species, some rather

Table 1. Body length and diameter of mouth on various fishes at post larval stage (by SHIROTA) classified into three kinds of feeding habit.

species	P			M			F		
	L	D	D/L	L	D	D/L	L	D	D/L
1	5.0	0.264	0.053	5.2	0.759	0.146	5.5	1.004	0.183
2	6.4	0.690	0.107	4.7	0.226	0.048	5.1	0.994	0.195
3	3.7	0.258	0.070	6.8	0.496	0.073	5.5	0.984	0.179
4	5.0	0.426	0.085	3.6	0.390	0.108	3.8	0.930	0.242
5	5.0	0.276	0.055	3.8	0.622	0.162	4.3	0.424	0.099
6	9.7	0.728	0.075	2.8	0.283	0.101			
7	4.4	0.291	0.066	6.6	0.882	0.134			
8	7.3	0.546	0.075	3.2	0.287	0.091			
9	9.2	0.550	0.060	2.8	0.223	0.079			
10	3.0	0.259	0.086	4.1	0.594	0.144			
11				3.6	0.303	0.084			
number of species	10			11			5		
average	5.9	0.429	0.073	4.3	0.461	0.106	4.8	0.867	0.180

P: Plankton feeder M: Mixed food eater F: Fish eater

L: Body length D: Diameter of mouth

P 1: *Konosirus punctatus*

P 2: *Etrumeus micropus*

P 3: *Engraulis japonica*

P 4: *Sardinops melanosticta*

P 5: *Spratelloides japonicus*

P 6: *Clupea pallasii*

P 7: *Harengula zunasi*

P 8: *Cololabis saira*

P 9: *Hemiramphus sajori*

P 10: *Oplegnathus fasciatus*

M 1: *Mugil cephalus*

M 2: *Ammodytes persanatus*

M 3: *Ilisha elongata*

M 4: *Trachurus japonicus*

M 5: *Scomber japonicus*

M 6: *Sillago sihama*

M 7: *Girella punctata*

M 8: *Siganus fuscescens*

M 9: *Platycephalus indicus*

M 10: *Chelidonichthys kumu*

M 11: *Fugu rubripes*

F 1: *Seriola aureovittata*

F 2: *Seriola quinqueradiata*

F 3: *Seriola purpurascens*

F 4: *Katsuwonus pelamis*

F 5: *Gadus macrocephalus*

important features become apparent: the mouth diameters //82
of the fish eaters are largely concentrated around 1 mm,
which is approximately twice the mouth diameter for fishes
with other feeding habits. Moreover, when we observe
the mean mouth diameter, we find it becoming progressively
smaller in the sequence: fisheaters, mixed food eaters,
plankton feeders -- which underscores the authors' original

Table 2. Body length and diameter of mouth on various fishes at post larval stage (by UCHIDA) classified into three kinds of feeding habit.

species	P			M			F		
	L	D	D/L	L	D	D/L	L	D	D/L
1	4.8	0.269	0.056	4.0	0.520	0.130	5.5	1.025	0.186
2	6.9	0.676	0.098	6.6	0.884	0.134	5.1	0.549	0.108
3	10.4	0.730	0.070	3.3	0.236	0.072	5.5	1.007	0.183
4	5.9	0.508	0.086	3.6	0.318	0.088			
5	4.4	0.372	0.085	4.1	0.614	0.149			
6	7.4	0.485	0.066						
7	10.7	0.550	0.051						
8	3.0	0.310	0.103						
number of species	8			5			3		
average	6.3	0.488	0.077	4.5	0.514	0.115	5.4	0.860	0.159

P: Plankton feeder M: Mixed food eater F: Fish eater

L: Body length D: Diameter of mouth

P 1: *Konosirus punctatus*

P 2: *Etrumeus microphus*

P 3: *Clupea pallasii*

P 4: *Sardinops melanosticta*

P 5: *Harengula zunasi*

P 6: *Cololabis saira*

P 7: *Hemiramphus sajori*

P 8: *Oplegnathus fasciatus*

M 1: *Scomber japonicus*

M 2: *Girella punctata*

M 3: *Siganus fuscus*

M 4: *Fugu rubripes*

M 5: *Chelidonichthys kumu*

F 1: *Seriola aureovittata*

F 2: *Seriola quinqueradiata*

F 3: *Seriola purpurascens*

expectation. A statistical determination was made of the relation between mouth diameters in fish eaters and in fish with different feeding habits and the results showed a 1% level of significance with Shirota's data and a 5% significant difference in the data from Uchida et al.

Secondly, the authors made a comparison of the ratios of mouth diameters to body lengths (D/L) broken down by feeding habits. As has been established, the size of the immediately post-hatching larvae shows no variation in accordance with feeding habits¹⁾, so if the mouth diameter

is larger, one may logically expect its ratio to body length to increase. As seen in Tables 1 and 2, the values for fish eaters were the highest, around 20%, followed by about 10% for mixed food eaters, and around 7% for plankton feeders. It is of some interest to note, however, that while in mixed food eaters and plankton feeders there was virtually no variation in direct comparisons of mouth diameters, the mixed food eaters showed a distinctly larger mouth diameter/body length ratio. A statistical determination of differences in mouth diameter/body length depending on feeding habits revealed a significant deviation at the 1% level for the data from both Shirota and Uchida et al. Both of the indices above indicate that the mouth diameters of fish eater ^{larvae} are markedly greater than those of fish with other feeding habits. Both the absolute values and the ratios to body length are larger. Moreover, the fact that the larvae of tunas, not included here, have large mouth diameters is well known, and clearly this fact shows that fish eater larvae are taking larger food than fish with other feeding habits, which means, moreover, that they are eating food larger in proportion to their own bodies.

Shirota⁵⁾ adduces further interesting data. Figure 1 represents changes in the upper jaw ratio (ratio of upper jaw length to body length) that accompany growth and the

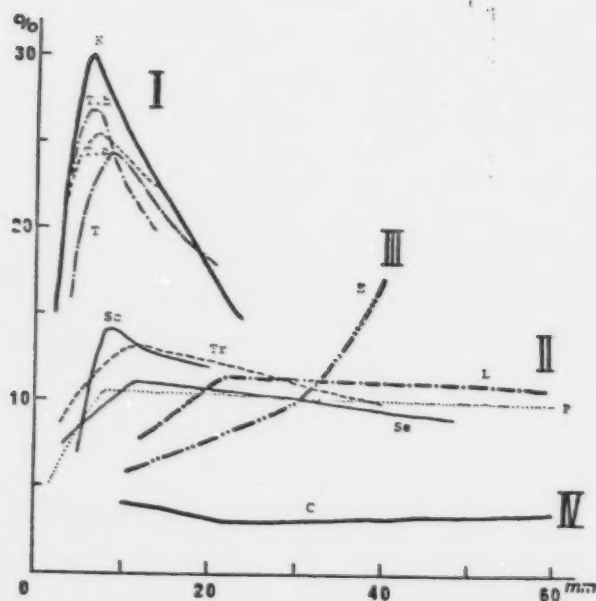


Fig. 1. Change of the ratio of upper jaw length to total length (by SHIROTA). T: *Thunnus thynnus* T.a: *Thunnus alalunga* T.b: *Thunnus albacares* K: *Katsuwonus pelamis* Se: *Seriola quinqueradiata* Tr: *Trachurus japonicus* Sc: *Scomber japonicus* C: *Cololabis saira* E: *Engraulis japonica* L: *Lateolabrax japonicus* P: *Pagrus major*

patterns of variation fall into four categories. Those with a sharp peak in the larval stage are Category I (skipjack, tuna); those with a blunter peak are Category II (mackerel, horse mackerel); those increasing towards the upper right are Category III (anchovies); those with no change are Category IV (saury pike)). Category I are obvious fish eaters and along with some of Category II the fish eaters exhibit a maximum upper jaw ratio during the post larval stage (roughly 5 to 10 mm) precisely when the authors hypothesize cannibalism to be at its height. This fact, considered in conjunction with the

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preceding investigations of mouth diameter, are thought to further reinforce the possibility of cannibalism among fish eaters in the post larval stage.

Population analysis of larval mortality due to cannibalism

Population variation model

As previously stated, the authors' larval mortality hypothesis may not apply to all fish eaters and, even in the species where it does apply, cannibalism may not account for the entire diet. For the sake of simplicity, however, we shall consider the case where the schools of a given species are reduced solely through cannibalism.

If the initial stock biomass is designated W_0 ; the number of fish in the initial stock, N_0 ; the weight per fish at that time, w_0 ; then we may write:

$$W_0 = N_0 w_0 \dots\dots\dots(1)$$

Assuming the entire school hatches, we designate by W_1 the stock biomass at the first total cannibalism after yolk absorption. Letting r be the weight increase of the larvae with respect to the mass ingested (feeding efficiency), we obtain:

$$W_1 = \frac{N_1}{2} w_1 (1+r) = \frac{1+r}{2} W_0 \quad //84$$

For the second complete cannibalism, we obtain

$$W_2 = \frac{N_2}{2} w_2 (1+r) = \left(\frac{1+r}{2}\right)^2 W_0$$

and for the n^{th} complete cannibalism

$$W_n = \left(\frac{1+r}{2}\right)^n W_0 = Q \cdot W_0 \quad (Q \leq 1) \dots\dots\dots(2)$$

Note that Q replaces $(1+r)/2$. This means that the stock biomass W decreases as an exponential function of the number of times of cannibalism. Fig. 2 shows the change in W_n/W_0 ^{accompanying} n when the values of r for each species are used. Where $r=1$, the graph will obviously become horizontal at the value 1.0 and it will steadily decrease for r values less than 1.

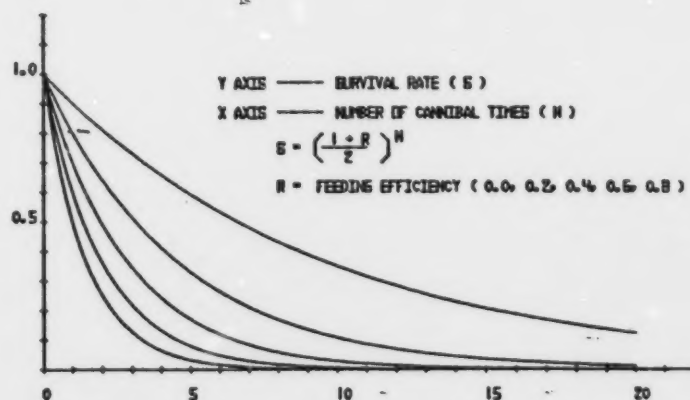


Fig. 2. Survival rate on larval fish with the number of times of cannibalism in various values of feeding efficiency.

Thus, during periods of universal cannibalism this will not result in an increase in stock biomass. Now, by formally differentiating W_n by n we obtain

$$\frac{1}{W} \frac{dW}{dn} = \log Q \quad \dots\dots\dots(3)$$

and since $\log Q$ is negative the decrease is taken as the rate of change $|\log Q|$.

Let us next consider the change in stock biomass W with respect to time. The number of times of cannibalism n does not invariably increase at identical time intervals and it may be somewhat more appropriate to take the predation volume as being proportional to time since we are dealing with the short post larval period. So, let us assume an increase in body weight of rw_0 per time of cannibalism and with the next cannibalism $(1+r)w_0$ will be consumed, and this will be continued, extending the time intervals before the next cannibalism by $(1+r)$.

With the first occurrence of cannibalism as the point of departure, let us assume a second occurrence after Δt . The time of occurrence of the n^{th} cannibalism

$$t_n \text{ will be } \begin{aligned} t_n &= \Delta + \Delta(1+r) + \Delta(1+r)^2 + \dots + \Delta(1+r)^{n-1} \\ &= \Delta \left(\frac{(1+r)^n - 1}{r} \right) \dots \dots \dots (4) \end{aligned}$$

Note; $t_1=0$, r in kg.

Solving this for n , we obtain

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$$n = \frac{\log(1+r)(1+\frac{r}{\Delta}t)}{\log(1+r)}$$

If this is substituted in Eq. (2) the change in stock biomass^W with respect to time t can be expressed as

$$W_t = W_0 \left(\frac{1+r}{2} \right)^{\frac{\log(1+r)(1+\frac{r}{\Delta}t)}{\log(1+r)}} = W_0' \left(1 + \frac{r}{\Delta}t \right)^a$$

where

$$W_0' = QW_0$$

$$a = 1 - \frac{\log 2}{\log(1+r)}$$

And since $0 \leq r \leq 1$, $a \leq 0$ and if $|a| = b$, we may write

$$W_t = \frac{W_0'}{\left(1 + \frac{r}{2}t\right)^b} \quad (5)$$

Thus, W is not an exponential function with respect to time but a negative power function. Fig. 3 shows changes in W_t/W_0 for $\Delta = 1$.

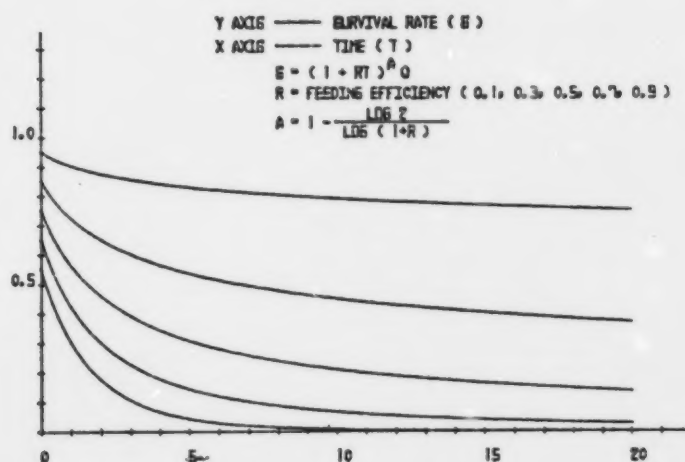


Fig. 3. Survival rate on larval fish with time in various values of feeding efficiency.

Model application to fish eaters

Skipjacks and tunas are typical of piscivorous fish. The post larval mouth diameter ratios, as shown in Fig. 1, are the largest for skipjack and tunas, so morphologically they exhibit a well-defined potential for cannibalism. The physiology and ecology of the larval stage, however, remain largely unknown, so they do not lend themselves to application of a model.

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On the other hand, with respect to yellowtail larvae, recent developments in culturing and experiments in artificial hatching and rearing have begun to shed considerable light on their physiology and ecology. In the area of cannibalism as well, Asami et al⁶⁾, for example, investigated the reduction of yellowtails by cannibalism in the larval stage and suggested that under various conditions 50 to 90% of mortality might be attributed to cannibalism. In addition, the Seto Inland Sea Fish Farming Centre succeeded in the large-scale artificial hatching and rearing of yellowtail in 1979 and it appears that the major cause of larval mortality in the experimental tanks was cannibalism. Moreover, Konishi⁷⁾ pointed out that there were spatial discrepancies between the yellowtail's natural spawning grounds and the nauplius distribution of the copepods which had been regarded as the primary food during the larval stage. Thus, yellowtail larvae, with slightly smaller mouth diameters than the skipjack/tuna group, do have considerable potential for cannibalism in terms of ecological data. Therefore, in this paper use is made chiefly of figures pertaining to yellowtail larvae, but the intention is to devise a model application for any fish eating species.

First is the estimate of r for the model application: generally, if a larva of body weight w_t is fed an amount of food F for time t , then we can estimate that

$$w_{t+1} = w_t + rF$$

$$r = \frac{w_{t+1} - w_t}{F}$$

A look at examples of yellowtail larva rearing shows this r value to be around 0.2 normally, with a higher value for smaller fish. For instance, when values using Ichimura's data⁸⁾ are plotted in Fig. 4, r is higher the smaller the body weight, and if an exponential curve is fitted, r is found to be between 0.2 and 0.3 for $w_t=0$. Naturally the value of r may vary depending on the quality of the food, but values of 0.2 to 0.3 appear reasonable in the light of rearing experiments with other fish as well. Therefore, this report assumes a feeding efficiency $r=0.25$.

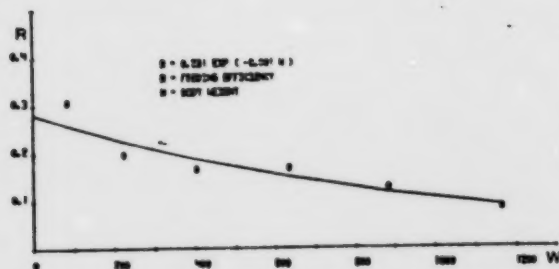


Fig. 4(a). Relationship between body weight and feeding efficiency of yellowtail in the culture pond (from ICHIMURA)—I.
Data in southern part of Uwa sea.

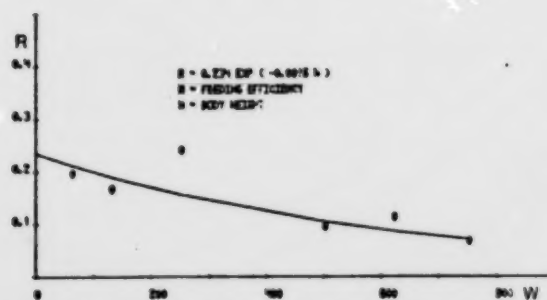


Fig. 4(b). Relationship between body weight and feeding efficiency of yellowtail in the culture pond (from ICHIMURA)—II.
Data in northern part of Uwa sea....

The post-larval body length in the case of yellowtail //87 larvae is estimated to fall within the interval between around 5 to 6 mm and 10 to 12 mm. Similarly, the skip-jacks and tunas are generally about the same size. More broadly speaking the hatching of a 1 to 1.5 mm diameter egg produces a π -fold 3 to 5 mm hatchling, which most commonly enters the post larval stage at 4 to 6 mm, remaining there until it doubles to 8 to 12 mm. In other words, growth in body length during the post larval stage is by a factor of two. If a cube rule is taken as applying to the body length/body weight ratio, then a doubling of body length will result in an eightfold increase in body weight and the relation

$$\frac{w_n}{w_0} = (1+r)^n = 8$$

will be valid.

Substituting $r=0.25$, as described earlier, yields $n=9.3$. This means that cannibalism is estimated to occur 9+ times in the post larval stage.

When these values are applied to the change in stock numbers, one finds

$$N_n = N_0 \left(\frac{1}{2} \right)^{9.3} = 0.00159 N_0$$

This indicates a survival rate of 0.16% in the post larval stage. A value of around 1/1000 has been given⁹⁾ for the yellowtail survival rate, estimated from the variety of

information scraped together so far and the previously estimated value does not differ from that by much. In other words, larval mortality can be explained by computing a mortality model based on cannibalism alone and the feasibility of the authors' hypothesis is thus indirectly sustained. The number of times of cannibalism n and the survival rates S for different values of r are shown in Table 3. One finds here as well that for a feeding efficiency between 0.2 and 0.3, S is between 0.04 and 0.4%, which is not at odds with the previously estimated survival rate.

Table 3. Number of times of cannibalism (n) and survival rates (S) at post larval stage in various values of feeding efficiency (r).

r	n	S
0.05	42.6	1.50×10^{-11}
0.10	21.8	2.74×10^{-7}
0.15	14.9	3.27×10^{-5}
0.20	11.4	3.70×10^{-4}
0.25	9.3	1.59×10^{-3}
0.30	7.9	4.19×10^{-3}
0.35	6.9	8.37×10^{-3}
0.40	6.2	1.36×10^{-2}
0.45	5.6	2.06×10^{-2}
0.50	5.1	2.92×10^{-2}

Moreover, in terms of stock biomass

$$\frac{W_n}{W_0} = \left(\frac{1+0.25}{2} \right)^{9.3} = 0.0126$$

indicating a biomass survival of 1.3%. In relation to time, one finds

$$t_n = \left(\frac{(1+0.25)^{9.3} - 1}{0.25} \right) \Delta = 21.5 \Delta$$

which means that for an eightfold growth in body weight in the post larval stage the time required is 21.5 times the interval Δ between the first and second cannibalisms. According to Konishi⁷⁾, in the case of reared yellowtail the duration of the post larval stage is on the order of 20 days and the amount of food ingested per day is roughly estimated at the rate of w_0 . So letting $\Delta=1$ and expressing t in days we find

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$$W_t = \frac{0.625W_0}{(1+0.25t)^{2.107}}$$

Discussion

A variety of inferences were attempted in this paper through the use of coefficients largely applicable to yellowtail but in certain respects one cannot regard yellowtail larvae as altogether typical of larval mortality through cannibalism. In fact, even in rearing experiments yellowtail larval cannibalism has been observed at lengths over 8 to 9 mm, which precisely coincides with the mouth diameter reaching its maximum ratio to body length, in

the vicinity of 10 mm. Up to that point, the larvae are reported to be small plankton feeders. Moreover, in the case of yellowtail larval cannibalism, they generally prey on fish smaller than themselves and there may be some problems with a model for cannibalism among fish of the same size. Shirota³⁾ estimates a cutoff body width of about 1.6 mm for food ingestible by 10 mm yellowtail larvae. This would mean they could eat only larvae of no more than 6 mm in length. In contrast, yellowfin tuna larvae have the capacity to cannibalize larvae of almost their own size. However, Shirota's calculations are based on a mouth aperture during feeding of no more than 75% (a 90° aperture is taken as 100%), so with a 100% aperture, yellowtail could also consume fish almost their own size.

The spawning grounds of fish eaters are generally in the offing and are not as rich in microorganisms as the areas very close to the shore. At the moment they first opened their eyes after birth the free-swimming organisms they saw around them were each other and their only choice was cannibalism or waiting to die where they were. If they were to wait and die, where would this great mass of dead fish, amounting to more than 99%, go? Observations so far have shown, in comparison with collections of larvae from the less than 1% survivors, the amount of dead fish

making up the more than 99% has been just about equal to zero. If they die, are they then eaten by fish of other species? But there is no need to prey on those larvae of large schools that have weakened or died. During their larval stage they themselves ought to be in the same situation as plankton. Or do they sink away? With this same sort of thing going on for many millions of years already, if one assumes more than 99% of the larvae sinking to the bottom, these supposedly offshore waters would certainly be pretty well eutrophicated by now. If we consider only the case of yellowtail in the waters around Japan, based on an annual catch of 40 to 50 thousand tons, there must be at least 20 to 30 thousand ^{tons of} parent fish. If the number is taken to be 20 thousand tons, there would be 10 thousand tons of females, and even with gonads making up 1/10 of the body weight, this would mean the release of 1000 tons of nutrient sources per year. This is scarcely realistic.

Finding cannibalism to be the cause of larval mortality in fish eaters permits numerous interesting logical deductions. For example, in terms of ichthyological evolution, the emergence of fish eaters generally occurs at a later stage than that of plankton feeders and when this fact is linked to the offshore distancing of habitats and spawning grounds, there appears to be some material

for speculation on evolution as related to fish ecology. We also suspect it may give one clue to the rational mechanisms whereby fish thrive in the nutrient-poor offshore waters. Furthermore, it may also offer one answer to the question of why, when land animals evolved in the direction of diminished fecundity and increased protective devices, marine Teleostei became progressively more prolific. It is our intention to discuss matters relating to ichthyological evolution in later papers, but we should like to emphasize here the necessity of regarding the larval mortality stage in fish not merely as a "time of trials" for them, but as an integral part of a rational developmental mechanism in fishes. This is also true in that this larval mortality is the greatest gateway to the study of fisheries resources.

In this series, the question was posed: "How is a fish-eating fish defined?". Kawai would prefer to define it not simply as a fish whose principal food is fish, but rather as a species of fish incapable of living, growing or reproducing without feeding on fish, in other words, a species of fish that has an ecological and physiological need to consume the flesh of fish. Such a precise definition cannot be made at this stage, however, so the definition "a species of fish that feeds chiefly on fish in the course of its life" is used. In that sense, it has

to be accepted as a provisional definition.

In the preparation of this paper, Mr. Tomoya TAKAHASHI kindly did a great deal of work in the compilation, computation and graphic representation of data, and we should like //89 to indicate our gratitude at this time.

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